A Description of Full Parental Genotyping

Report Submitted to the Pacific Salmon Commission

Eric C. Anderson* John Carlos Garza*

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Summary

This report describes how full parental genotyping (FPG) could be implemented as an alternative, or complement, to coded wire tagging (CWT) of hatchery salmon in the Northeast Pacific. The FPG method works by genotyping the broodstock at hatcheries and including their genotypes in a database (the *parent database*) from salmon spawned each year. The genotypes of fish sampled in fisheries, at hatcheries, or on natural spawning grounds can be compared to those in the parent database. With a sufficient, and surprisingly modest, number of genetic markers, the exact parents of any sampled fish can be identified, provided the parents' genotypes are in the parent database. Knowledge of the parent pair producing a recovered fish provides managers and biologists with the hatchery of origin *and* the cohort of the recovered fish—precisely the information provided by a coded wire tag recovery and required for implementing current CWT-based cohort reconstruction models for fisheries management. Thus, the FPG method can provide managers with all of the same information as the CWT program. In addition, an FPG program would have considerable collateral benefits. Most notably:

- The per-fish tagging cost of FPG would be considerably lower than that of the CWT program, and a *much* higher proportion of adipose-clipped production could be tagged; All juvenile production from FPG hatcheries would be tagged.
- The higher proportion of tagged fish may eliminate the need for a secondary, electronic tag detection method in sampling of harvest or in escapement.
- Heads of recovered fish need not be removed; only a small piece of fin must be collected and sent for genetic analysis.
- The parent database could easily be integrated into a genetic stock identification (GSI) database that shares molecular markers, allowing both adipose-clipped, but non-FPG, and naturally spawned fish to be identified to stock, and sometimes cohort, of origin. Such an integrated FPG and GSI system would provide information about stock of origin for every sampled fish, marked or unmarked.

The most important potential limitations of the FPG method are *i*) it is most cost-effective for cohort-based management only when a large proportion of adipose-clipped fish are offspring of parents in the parent database, *ii*) it will be difficult to "tag" natural spawning fish via FPG, because it is not easy to capture the majority of natural-spawning salmon and include them in the parent database (however, GSI analysis could yield stock of origin and, in some cases,

*Southwest Fisheries Science Center, National Marine Fisheries Service, 110 Shaffer Road, Santa Cruz, CA 95060

the cohort of natural spawning fish), and *iii*) since the proportion of FPG-tagged fish from all hatcheries would be high, it is not possible to enrich the representation of fish from "weak" stocks amongst all tagged fish. However, it is important to note that the absolute number of tagged fish from "weak" stocks will be greater with FPG, with essentially all fish from such stocks tagged.

1 Introduction

Since the late 1960's coded wire tags (CWTs) have been used to track salmon released from hatcheries and, occasionally, fish produced on natural spawning grounds. CWTs are mechanically implanted in the heads of juvenile fish and each tag contains a code that is unique to each release cohort and location (hatchery). Tagged fish receive an externally-visible adipose fin clip which aids in the recovery effort of the tags. Until 1996, the only fish with an adipose fin clip were those that also carried a CWT. Since that time, federal and state laws and regulations have been enacted that require the mass marking (with adipose fin clips) of most hatchery production. This would enable the administration of mark-selective fisheries, in which only hatchery fish bearing the adipose fin clip are retained, and unmarked (presumably wild) fish, if caught, are released. Such mass-marking presents a serious challenge to the use of CWTs for fisheries management, because finding a CWT amongst the fin clipped fish becomes a needle-in-a-haystack problem and a great many fin clipped fish may have to be screened to find one with a CWT.

The Pacific Salmon Commission has convened a panel of experts to explore ways of updating, complementing, or replacing the CWT system to deal with the problem of mass-marked hatchery production and consequent mark-selective fisheries. Prior to the formation of this panel, the primary proposal for amending the CWT system has been to implement a program of electronic survey, outfitting field sampling crews in fisheries and hatcheries with metal detectors to screen a large number of (mostly adipose-clipped) fish to find the ones carrying CWTs. Such a program would incur very high initial capital costs and substantial annual labor costs. Another strategy is to tag a higher proportion (perhaps all) of the fish receiving adipose fin clips, so that the hatchery and cohort of any adipose-clipped fish that was recovered could be identified. This would eliminate the need for electronic detection. However, it would be cost prohibitive, because of the enormous number of hatchery produced juveniles and the cost of tagging fish with CWTs.

We propose an alternative to tagging with CWTs called "full parental genotyping" (FPG). It uses genetic analysis, but, unlike better-known genetic stock identification (GSI) methods, it provides both stock of origin and the cohort for recovered fish. FPG relies on the simple principle that if you identify where and when the parents of a recovered fish spawned, you will obtain the location and cohort of origin for that fish. Identifying the exact parents of recovered fish is done by comparing the genotype of the recovered fish to the genotypes of possible parents and identifying the exact parent pair through traditional parentage analysis. Because FPG is most easily implemented in a hatchery, which is precisely where both current CWT programs and mass marking is occuring, it is feasible with FPG to tag most hatchery production and therefore most mass-marked fish. Our analyses have shown that FPG can be implemented at a cost that would be competitive with the current CWT program and, possibly, less than that of a CWT program with electronic detection. We describe the results of these analyses and discuss the advantages and limitations of FPG.

The following section briefly discusses parentage analysis, single nucleotide polymorphisms, and the number of genetic loci that would be required to implement FPG with low error rates. Section 3 discusses how and why the cost of tagging individuals via FPG is less than that of coded wire tagging, and Section 4 discusses the cost of tag recovery using FPG relative to that of CWT. Section 5 discusses how the genotyping done for FPG could be used in a GSI context, as well as an FPG context. Section 6 considers what additional steps should be taken to make FPG as useful as possible in the context of recovering fish from weak stocks, and Section 7 discusses how FPG would work within the context of a double index tagging approach. Finally, Section 8 describes the additional, useful information that would come from the FPG approach and Section 9 discusses what steps have been taken toward developing the molecular tools required for FPG.

2 Parentage Analysis, SNP markers, and number of loci

The application of FPG first requires determination of the genotypes for the parents (broodstock) of all fish from a particular hatchery cohort. These genotypes are recorded in a *parent database*. Later, when a fish is sampled in a fishery or in the escapement, its genotype is compared with every parent pair in the parent database from spawning years that could possibly have given rise to that fish, to determine its exact parents. This assignment of individuals to parents is an example of pedigree reconstruction. Parentage analysis and other methods of pedigree reconstruction with molecular genetic markers have been used routinely in human populations and natural populations of plants and animals since the 1970's. Most of the statistical methodology for parentage analysis was pioneered in a classic paper in the 1970s (Thompson 1976), and was later expanded upon to address the nuances of pedigree reconstruction in natural populations (Meagher and Thompson 1986; Thompson and Meagher 1987).

As applied to FPG, parentage analysis using a likelihood approach is relatively straightforward. Briefly, imagine that we wish to test whether an ordered trio of individuals (y, m, f) represents a youth (y) and its mother (m) and father (f). Given the frequencies of different alleles at different genetic loci in the population, it is possible to compute the probability $L(Q)$ of the genotypes of the trio under the assumption that they are a youth-mother-father family. It is also possible to compute the probability $L(U)$ of the trio under the assumption that they are, in fact, all unrelated individuals (or any other combination of related and unrelated individuals). The test statistic $\Lambda = L(Q)/L(U)$ is useful for identifying trios that are true youth-mother-father families. For such "correct" trios, Λ will be large, and a critical value Λ_c can be used to classify trios into "correct" and incorrect categories. In other words, if Λ for a certain trio was greater than Λ_c you would conclude that the parents of y were indeed m and f. If however, Λ for that trio was less than Λ_c, you would conclude that m and f were not the parents of y. By approximating the distribution of Λ for youth-mother-father trios and for unrelated trios, it is possible to compute the probability that an unrelated trio will have a Λ greater than Λ_c and also the probability that a "correct" trio will have a Λ less than Λ_c. These values give the per-trio probability, α, of false-positives (declaring m and f the parents of y when they are not) and the per-correct-trio probability, β, of false negatives (declaring m and f are not the parents of y when, in fact, they are), which can be used to determine how many genetic marker loci would be needed to perform FPG accurately.

In parentage analysis with genetic markers, a low laboratory error rate is crucial, as such errors

can result in mismatches between true parents and offspring, which can incorrectly decrease Λ. We propose using a type of genetic marker locus for FPG called a single nucleotide polymorphism (SNP), which has a low laboratory error rate. Another confounding factor for many commonly used genetic markers, particularly microsatellites, is that mutations arising during meiosis appear as mismatches, which can, again, incorrectly decrease Λ. The per-locus mutation rate of SNP markers is several orders of magnitude lower than that of microsatellites, and fewer mutations are thus expected to appear in individuals tagged with FPG using SNPs than using microsatellites, which currently dominate pedigree reconstruction efforts.

SNPs typically have only two alleles, and these alleles represent the absolute nucleotide state of the marker (as opposed to relative size or gel mobility, as with microsatellites and allozymes) which makes it possible to determine the genotype of each locus with minimal human interaction. This makes them amenable to high-throughput, automated genotyping, and means it is far easier to standardize markers between different laboratories. The only drawback from an analytical perspective is that SNPs, with only two alleles, have less statistical power per locus for parentage analysis than markers like microsatellites, which may have as many as 100 alleles (*e.g.*, Glaubitz *et al.* 2003). However, the potential efficiency and lower cost of SNP analysis, as well as the substantially lower laboratory error and mutation rates, lead us to believe that they will be a far superior choice for FPG applications.

An important remaining question is how many SNP markers are required to conduct FPG on a coastwide scale. We have undertaken a series of power analyses addressing this question (Anderson and Garza, ms in prep). The most relevant findings of these analyses are: *i*) the false positive rate decreases exponentially with the number of SNP markers used, so it is impossible that the tagging program could ever grow so large that parentage error rates could not be diminished adequately by adding a modest number of additional SNP markers, and *ii*) a set of about 100 SNPs in which the frequency of one of the alleles varied between .2 and .8 is sufficient to have a false negative rate of less than 10% (meaning that 90% of FPG-tagged fish could be assigned to parent pairs) and the false positive rate would be low enough that of all individuals, coastwide, assigned to a parent pair via FPG, you would expect that virtually no individuals would be assigned to an incorrect parent pair.

3 Tagging Operations and Costs

Tagging fish by FPG involves genotyping their parents at hatcheries. Operationally, it proceeds as follows: at each hatchery producing fish contributing to a fishery, a tissue sample (a small fin clip, for example) is taken from every male and female spawned to create the next generation. Those fin clips are sent to a central laboratory (or one of several laboratories), where the genotypes of the fish are determined. These genotypes then go into the parent database, along with the dates that the fish were spawned and any information about which males had been mated to which females.

Optimally, all matings would be recorded at the hatchery, and the fin clips of all broodstock individuals would be linked to the mating information. This would reduce the number of possible parent pairs that had to be evaluated in the search of the parent database and, therefore, the number of genetic markers necessary to assign parentage at a given total error rate. However, if

that requires too much work or attention by hatchery staff, another alternative would be to have hatchery staff prepare a number of ethanol-filled receptacles beforehand and label them with date of spawning. Then during spawning operations, they would place fin clips from all males spawned each *day* into one receptacle and fin clips from females into another. It would be unnecessary for the hatchery staff to record the actual matings or any other information in this scenario. The tradeoff is that the number of possible parent pairs to be searched in the parent database would increase (the number of possible matings each day is just the number of unordered pairs of male and female samples each day), but the absolute number of false positives incurred by examining the extra parent pairs could be held constant by simply adding approximately 8 additional genetic markers to the analysis. With this alternative, there is some possibility that multiple fin clips from a single male might be taken and deposited in the receptacles, but this would easily be recognized from the genotype data, and the duplicate samples would be discarded.

The per-offspring tagging cost using FPG is much less than that using CWTs because by genotyping a single parent pair you are "tagging" *all of the offspring that the pair produces*. This eliminates the need to physically implant tags in any juvenile fish (though they will presumably be mass-marked by adipose fin clipping). A rough comparison of tagging costs for chinook salmon using the two methods can be made by making a few assumptions. Imagine that it costs $\$F$ to genotype a single adult salmon at the number of loci required to do FPG. Let each female salmon at the hatchery produce, on average, d juveniles that survive to the age of release, and let the number of males spawned at the hatchery be equal to the number of females. Under these assumptions it costs, on average, $\$2F$ to tag d juveniles by FPG, or, the per-juvenile tagging cost of FPG is about $\$2F/d$. By comparison, if it costs $\$C$ to tag 1,000 juveniles with CWT, then the per-offspring CWT tagging cost is $\$C/1000$. Now, suppose that we wish to determine what the genotyping cost F must be so that we could tag ten times[1] more fish by FPG than by CWT. Then, the cost, per juvenile, of tagging with FPG must be one tenth that of tagging by CWT. This would be the value of F satisfying:

$$\frac{2F}{d} = \frac{1}{10} \times \frac{C}{1000} \quad \Longrightarrow \quad F = \frac{dC}{20000}$$

Numerical values for C are not well known. Estimates in the literature range from \$70 to \$130 per 1,000 fish for coded wire tagging. Let's use $C = \$100$. Chinook salmon are highly fecund and egg to smolt survival is typically fairly high in hatcheries, so we will use $d = 4000$. Using these figures, we conclude that if it is possible to genotype fish for \$20, then *ten times* as many fish can be tagged with FPG as with CWT for the same price.

Currently the cost of consumables used in genotyping a SNP locus with the Applied Biosystems Inc. SNP-plex genotyping system (one of several instrument/reagent platforms available) is approximately \$0.06 per SNP. For a 100 SNP panel, the consumables cost is thus \$6. For microsatellites, a reasonable estimate of the additional genotyping costs (labor, *etc.*) is twice the consumables cost (Paul Moran, pers. comm.). This is likely an overestimate for SNPs which are less labor intensive, but, nonetheless, that gives us \$18 as the cost of genotyping a fish with a 100 SNP panel. If we add

[1]We show this calculation for a factor of ten, because, though it seems accurate numbers are difficult to come by, we have been told that if mass marking of hatchery fish occurs, then roughly only 10% of adipose-clipped fish will carry CWTs. Therefore, if you can tag 10 times more fish, then you can tag most if not all of the mass-marked production. Hence, we are presenting the cost of genotyping required in order to be able to tag all of the mass-marked production by FPG for the cost of coded wire tagging only 10% of it. If the proportion of CWT'ed fish amongst all mass marked fish would be different, then it is obvious how the calculation should be amended.

the reasonable figure of $2 per fish for transporting and extracting the DNA, we have $20 per fish as a cost that could be reasonably achieved today for a 100 SNP panel. In addition, this cost is several times the current cost for SNP genotyping in humans and model organisms, so the cost of SNP genotyping in salmon is likely to fall substantially in the future as it becomes more widespread and more capital (equipment) investment is made by managing agencies.

4 Recovery Operations and Costs

Recovery of FPG tagged fish in harvest, in escapement, or as strays to spawning grounds will proceed much as it does today for adipose fin-clipped CWT fish. However, instead of sending heads to a head lab, fin clips will be sent to a genetics lab for DNA extraction and genotype determination. A potential major benefit of an FPG program is that it would not be necessary to electronically survey mass-marked fish because each fish missing an adipose fin, and from a hatchery in which the broodstock had been genotyped, would contain a tag that provides information about origin and cohort. Of course, the magnitude of this benefit depends upon the proportion of hatchery production for which broodstock genotypes are included in the parent database.

Recovery of tagged fish at the hatcheries in an FPG program would provide an additional efficiency relative to a CWT program. This is because either all or a large proportion of the fish that are genotyped as part of the effort to tag fish, can also be used as tag recoveries from the escapement. Because of this, the hatchery staff should select fish for spawning as a random sample from the fish arriving at the hatchery during any time period. This would ensure that the FPG tag recoveries that are gained in the process of genotyping the fish spawned at the hatchery are a random sample of the tags coming back into the hatchery, as well as preventing a possible mechanism for hatchery selection. Depending on the proportion of fish returning to hatcheries that are used as broodstock and the amount of escapement sampling necessary, it might also be important to sample (*i.e.*, genotype) some proportion of returning adults that are not spawned.

Although the cost of recovering and decoding a CWT is not well known and likely quite variable, the cost of genotyping a fish (to recover its FPG tag) will likely exceed the cost of decoding a CWT from that fish. Quoted costs per fish of decoding a CWT vary from $3-$5 per fish (Hammer and Blankenship 2001) to $11 per fish (Bowhay 2004), whereas the current cost of providing a 100 SNP genotype is approximately $20, although it should be much lower within the next decade. Moreover, the CWT costs cited above are without electronic sampling, which, when taken into account, may make the current cost of tag recovery for the two methods roughly similar. When the overall costs of tagging (lower with FPG) and tag recovery (likely higher with FPG) are taken into account, an FPG system should compare favorably with a CWT system, particularly if some value is placed on the collateral information gained by FPG (see Section 8).

5 Integration with Genetic Stock ID

One of the primary advantages of FPG is that it is easily integrated into a management regime that uses both FPG, for participating hatcheries, and genetic stock identification (GSI), for naturally

spawning and non-FPG hatchery populations. A subset of the genetic markers used in FPG can be used for GSI in an initial genetic assay that assigns fish to stock of origin, with each of the FPG hatcheries representing a stock. Those fish not assigned to an FPG (indicator) hatchery, will be identified to stock of origin. Those assigned to an FPG hatchery with genotyped broodstock would then be subject to genotyping of additional markers to determine specific parents and, therefore, cohort. Such a system could accomodate any proportion of marked/unmarked fish, thus allowing the same set of genetic markers to be used in a sequential genotyping effort that provides stock of origin for all fish, marked or unmarked, as well as cohort of origin for fish from FPG hatcheries.

Moreover, it is frequently possible to accurately assign fish to a particular stream/population of origin *and* cohort/broodyear with a simple GSI and data from 15-20 microsats and 50-100 samples per cohort. There is apparently substantial variation in allele frequencies from year to year in many salmonid populations, which seems to be higher in smaller (weaker) stocks/populations. It may, therefore, be possible to type a modest number smolts or carcasses from "weak stocks" with no FPG hatcheries each year and use those in a relatively large GSI effort on both marked and unmarked fish to provide the tag recoveries for weak stock, cohort-based management.

It will cost several million dollars each year to implement such fishery sampling along side an FPG system for hatcheries, but it will allow identification of *all* fish from any weak stock that you can sample with a trap or carcass survey. It will likely provide small recoveries for many/most stocks, but there will be *some* recoveries for many more stocks than with the current system. Such a combined GSI/FPG system can also easily be scaled (*i.e.*, number of fishery samples) to the level of precision needed/tolerable to management agencies. Such a system would also provide better management for weak stocks not associated with indicator hatcheries, which, by design, are completely missed by the current management regime.

At many hatcheries, a modest fraction of all returning adults are used as broodstock with the additional fish turned back into the river, either above or below the hatchery. When these fish are handled, a small tissue sample can be taken and a genotype obtained, thereby providing tags for all of that individual fish's offspring. This will allow direct evaluation of the assumption of current management strategies that the tagged hatchery release groups are representative of associated naturally-spawning stocks.

6 Weak Stocks

The estimation of fishery- and cohort-specific impacts on rare, or weak, salmon stocks is difficult using any tagging program, because their relative scarcity makes substantial numbers of tag recoveries unlikely. Traditionally, the CWT program has scaled the tagging rate of such weak stocks, such that a greater proportion are tagged and the probability of recovering a tag from a weak stock is similar to that of more abundant stocks. While FPG does not provide a specific mechanism to enhance the tagging rate of such weak stocks, it offers the advantage that all fish produced at hatcheries representing weak stocks would carry a tag. The estimation of parameters for fishery management would then require a larger fishery sample with FPG than with a CWT + electronic detection program, but the cost of typing a larger fishery sample would be offset by the savings from eliminating electronic detection. It might also be possible to use an additional external tag on

only the weak stocks, so that they are readily identifiable in a mixed fishery context. Moreover, the use of an integrated FPG/genetic stock identification system (see previous section), would provide information on fishery impacts on weak stocks not represented by FPG hatcheries.

7 Estimating Incidental Mortality

In a mark-selective fishery (MSF) only those fish bearing a mark (*e.g.*, an adipose fin clip) are retained. Unmarked fish are released in the hope that they will survive either to be caught in a non-mark-selective fishery, or to spawn. MSFs have the potential to reduce fishery impacts on small, weak stocks (which would not be marked) while still allowing exploitation of fish from large hatchery stocks producing marked fish. However, it is challenging to assess how well MSFs achieve their goal, because it is difficult to estimate the additional mortality that unmarked fish may experience due to being caught and released in an MSF. This additional mortality is termed "incidental mortality."

The method of *double index tagging* (DIT) offers a way to estimate incidental mortality. In the DIT protocol, fish bearing CWTs are released in two different groups—a marked and an unmarked group. The tags in these fish are then recovered in fisheries and in escapement by electronic detection of CWTs, allowing the estimation of incidental mortality rate of each cohort in different years, given some assumptions about marine survival. At least one of the proposals for the analysis of DIT data (Hankin 2004) explicitly requires that CWT (or FPG) recoveries be made from marked *and unmarked* fish in the non-mark-selective fisheries. (A directed graph showing the underlying cohort model and assumptions of that proposal appears in Figure 1). A useful feature of CWTs in this context is the fact that they may be electronically detected (albeit at substantial cost) amongst samples of both marked and unmarked fish, facilitating the recovery of CWT in both types of release groups. In contrast, if a fish in an unmarked release group were tagged solely using FPG, there would be no way of verifying its hatchery and cohort, (or even of verifying that it was descended from parents of known genotype) without genotyping the fish. If there are many unmarked fish in the fisheries that do not originate from FPG hatcheries, then it would be impractical to genotype many of them to recover a small number of FPG-tagged fish.

For the above reason, FPG would be most effectively applied in the DIT framework if another, sequestered, preferably externally visible, method of marking the non-adipose-clipped DIT release group was available. For example, if the non-adipose-clipped DIT release groups were clipped on the ventral or pelvic fins, the amount of genotyping necessary to fully implement DIT by FPG would be greatly reduced. Alternatively, both DIT groups could be tagged by FPG, but the marked group fish could have CWTs implanted in them so that they can be detected in electronic surveys of unmarked fish in the fisheries. This scenario could confer cost savings because it would be unnecessary to electronically survey adipose-clipped fish, and the electronic sampling effort for non-adipose-clipped fish could be focused on fisheries most relevant to the DIT study design. Depending on the sizes of two DIT release groups, and the recovery rate, it may be cost effective to implant inexpensive blank wire that can be electronically detected into the unmarked individuals, and recover their stock and cohort via FPG. This will be particularly true as genotyping costs continue to fall.

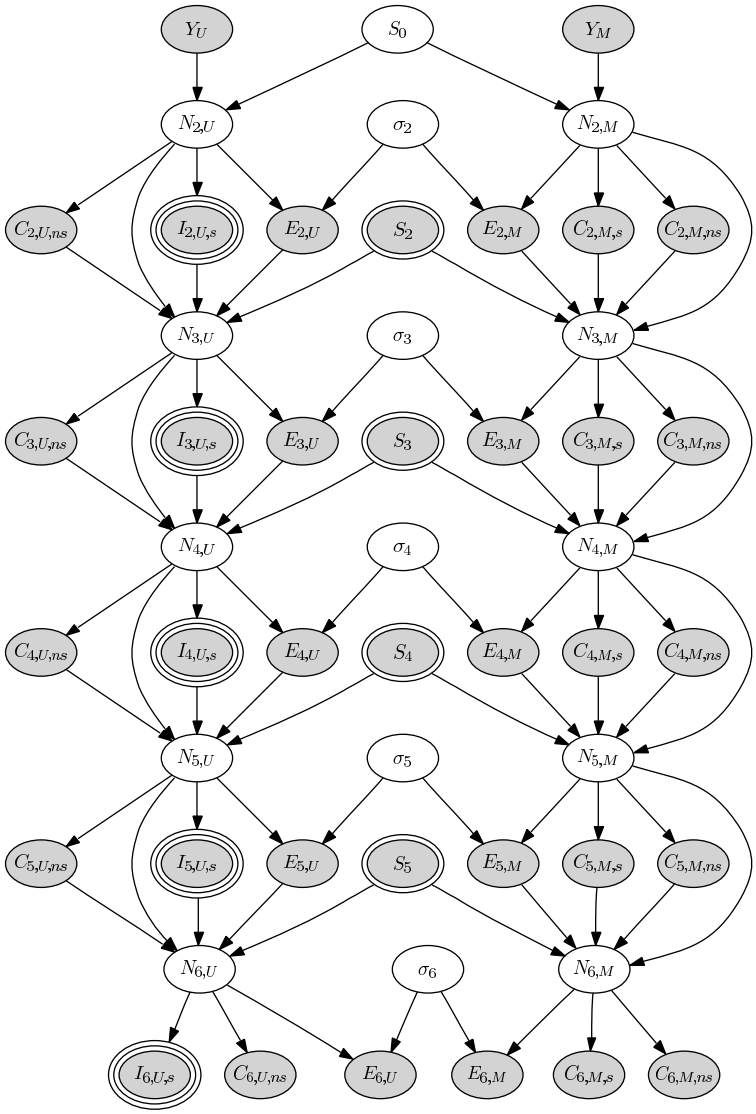

Figure 1: Directed graphical model depicting Hankin (2004)'s incidental mortality estimation method using double index tagging. Gray nodes with a single periphery are quantities for which estimates are assumed to be available. Gray nodes with two peripheries are variables whose values are assumed to be known. Gray nodes with three peripheries are the incidental mortalities that are to be inferred. The unshaded nodes are unobserved, latent variables/parameters. An M subscript refers to the marked (adipose-clipped) group, and the U subscript refers to the unmarked (non-adipose-clipped) group. Y is the number of fish released. The $N_{a,\cdot}$'s are numbers surviving to age a, and the $E_{a,\cdot}$'s are escapements of each group at age a. The $C_{a,\cdot,ns}$'s are numbers of fish of age a caught in non-mark-selective fisheries and the $C_{a,M,ns}$'s are numbers of marked fish of age a caught in MSFs. The $I_{a,U,s}$'s are the incident mortalities of age a unmarked fish in MSFs. σ_a is the probability that an a-year-old matures. This graph explicitly shows the assumptions that the survival to age 2 is identical for the M and the U groups, and also that the age-specific maturation rates are identical for the two groups.

Another approach to DIT that would be more attractive in an FPG framework would be to develop estimators for incidental mortality that do not rely on independent estimates of the number of unmarked DIT release fish captured in non-mark-selective fisheries. This would eliminate the need for visual or electronic sampling, or genotyping, of unmarked fish recovered in fisheries. Rather, unmarked fish in the escapement to each stock could be genotyped and the relative escapement rates of marked and unmarked groups could be used in a latent variable model to estimate incidental mortality. Such an analytical method would not allow estimation of separate incidental mortality rates associated with each cohort in each particular fishery; however, for many stocks it may be difficult, if not impossible, to obtain precise estimates of fishery- and cohort-specific incidental mortality anyway. Alexandersdottir *et al.* (2004) noted that the per-fishery exploitation rates for most stocks can be estimated only to within a standard error of well over 25% using CWT recoveries. Propagating that much uncertainty through the graph of Figure 1 while trying to estimate the variables at some of its nodes, raises the question of whether it is possible to accurately estimate incidental mortality rates in specific fisheries (Hankin 2004).

In spite of the difficulty in estimating fisheries-specific incidental mortality rates for many stocks, it is still possible to obtain useful information about the efficacy of MSFs. The most important measure of how well MSFs are working is the overall survival or escapement rate of unmarked fish relative to marked fish. For estimating this quantity in any stock, the FPG approach has the following benefits: 1) it is possible to economically tag most if not all of a hatchery's production using FPG, 2) a portion of the FPG tag recoveries at the hatchery will entail genotyping that will be done anyway (for tagging the next generation)—this provides economical FPG tag recoveries of marked and unmarked DIT groups in the escapement, and 3) the proportion of unmarked fish in the escapement that represent the unmarked DIT group should be much higher than in fisheries, thus alleviating the need for excess genotyping of unmarked fish.

8 Additional Information from FPG

As outlined above, the FPG method provides all of the same information as a CWT system and is, thus, a suitable alternative for cohort reconstruction-based fishery management. However, since the FPG method identifies the exact parents of a sampled fish, it actually provides much more information than stock and cohort of origin. Specifically, it allows the evaluation of a host of life history, ecological and quantitative genetic questions, such as the heritability of age at reproduction and disease resistance/susceptability, as well as an evaluation of hatchery domestication, estimation of effective size, and many other biological topics. The ability to collect large samples from fisheries and in escapement will also dramatically increase knowledge of marine distribution patterns and of marine survival.

9 How Far Along are We?

One of the main obstacles faced in evaluating and implementing FPG is that few SNPs have been discovered and converted to usable assays in salmon. There are fewer than 50 markers in use for each of the Pacific salmonid species. However, this is changing rapidly, both through the efforts

of multiple individual labs and because the Chinook Technical Committee of the PSC has recently awarded a modest amount of money to several genetics labs to develop and evaluate at least an additional 30 SNP markers. The human genetics community developed several million SNP markers over the last decade, once their utility and advantages were clear, and it should be a relatively trivial undertaking for salmon geneticists to develop several hundreds.

An additional area in which human genetics suggests what is possible for SNP genotyping in salmon management is through the dramatic reduction in costs that has been achieved by dedicated genotyping centers. Such centers produce a single SNP genotype for \$0.01–0.02 on a contract basis, although this is after the cost of the capital equipment necessary to outfit the genotyping centers.

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